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GERMPOOL UTILIZATION: *GOSSYPIUM*, A CASE HISTORY

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GERMPOOL UTILIZATION: *GOSSYPIUM*, A CASE HISTORY

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By Paul A. Fryxell[1]

ABSTRACT

Selected examples of the successful utilization of the *Gossypium* germpool demonstrate both the actual value in the past and the potential value for the future of germplasm collections. Valuable traits have been transferred to commercial varieties from wild or primitive cottons, and new types of plants have been created by the genetic manipulation of materials in the germpool. Examples of useful phenotypes previously unknown in the genus include rust-resistant Upland cottons, transgressive segregants for root-knot nematode resistance, and a broad range of glandless cottons. The importance of maintaining and expanding the germpool is emphasized.
KEYWORDS: cotton, cytoplasm, disease resistance, germplasm, gossypol, pest resistance, plant breeding, polyploidy.

INTRODUCTION

In the course of human history and prehistory, four species of cotton have been domesticated and brought into large-scale cultivation in different parts of the world. The evolution of these crop species, of course, continues at the present time at both the diploid and tetraploid levels (*5*).[2] As a consequence of this history, diverse *Gossypium* germplasm is available for breeding, from the highly improved cultivars of present-day intensive agriculture to the remnants of less productive types that were formerly (and in some places still are) grown in primitive agriculture, to the feral and wild forms that still exist in certain parts of the Tropics.

In addition to the germplasm just indicated, the genus *Gossypium* encompasses even wider variation in the wild species. There are approximately 30 wild species, all diploids, that are native to North and South America, Africa, the Arabian Peninsula, and Australia. These wild diploids inhabit generally arid habitats, are highly diverse in morphological and other characters, are genetically diverse, and are widely separated by their evolutionary history.

As is well known in other crops, distantly related wild species offer tantalizing opportunities of transferring useful characters to domesticated species; but at the same time there are formidable difficulties in effecting these transfers (see Meyer, *13*). In many crops the promise of utilizing such desirable characters in plant breeding has remained just that— a promise, a hypothetical possibility never accomplished.

It is my purpose here to bring together, for the genus *Gossypium*, cases where the *Gossypium* germpool has been used successfully to introduce agriculturally useful characters into primary breeding stocks and commercially acceptable cultivars. My examples are not exhaustive: rather I wish to illustrate how germplasm collections are *actually* useful, not simply *potentially* useful.

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[2] Italic numbers in parentheses refer to items in "Literature Cited" at the end of this publication.

SIMPLY INHERITED CHARACTERS

Simply inherited characters are most easily transferred to agricultural strains by backcrossing. The ease of transfer depends strongly on how distantly related the source of the desirable gene is. When this source is one of the wild diploid cotton species, the difficulty can be considerable. A good example is resistance to cotton rust disease, successfully bred into agricultural cottons by L. M. Blank.

Cotton rust is caused by *Puccinia cacabata* Arth. & Holw., a heteroecious rust that alternates hosts between *Gossypium* and certain species of the grass genus *Bouteloua* that are native to the area where the disease occurs. The pycnial and aecial stages develop on the cotton host and cause the disease symptoms (*1*).

The disease occurs in the cotton-growing areas of northern Mexico and the Southwestern United States. Its severity varies from year to year, and its incidence, even in bad years, is irregular, because disease development strongly depends on local climate. The disease is present to some extent almost every year, but it does significant economic damage in only about one year out of five. In such years, it may cause as much as 90 percent loss in individual localities, but relatively little loss in the general area. Thus, it is a problem that would be much better met by a genetically resistant variety than by repeated treatment with costly fungicides that are only sometimes needed and which are only effective under certain conditions of timing of application and microclimatic variation.

Blank developed standardized greenhouse inoculation techniques that permitted him to survey a wide range of germplasm for resistance to cotton rust. He found no resistance in *G. hirsutum*—among agricultural varieties, primitive race stocks, or wild forms. A survey of the available diploid species, however, revealed a few sources of resistance, although most were susceptible. Strong resistance was found in the wild *G. anomalum* Wawr. & Peyr. from Africa and in the cultivated diploid *G. arboreum* L.

To transfer this resistance from the diploid species to the tetraploid *G. hirsutum* L., it was necessary to use artificial polyploids involving these species. One method involved the hexaploid of the direct hybrid (fig. 1). This hexaploid was fertile and could be crossed with the tetraploid *G. hirsutum* L. to produce a pentaploid. Continued backcrossing to *G. hirsutum* L. resulted in a return to the tetraploid chromosome number. Alternatively, synthetic tetraploids could be crossed directly to *G. hirsutum* L. and subsequently backcrossed (fig. 2). Appropriate screening and selection insured that the desired genes were introduced into the new material. With such materials and by such pro-

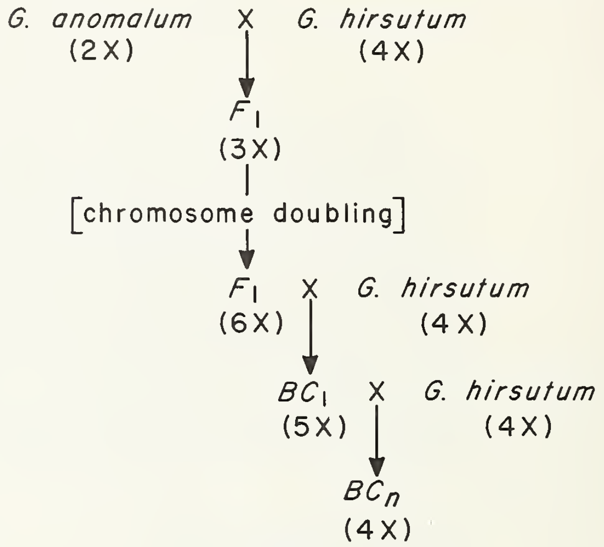

FIGURE 1.—Pedigree illustrating the method of introgressing germplasm from a diploid species into a tetraploid species via an artificial hexaploid.

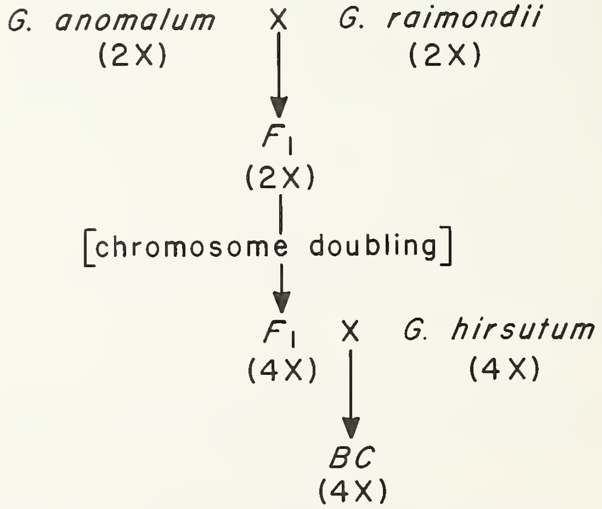

FIGURE 2.—Pedigree illustrating the method of introgressing germplasm from a diploid species directly into a tetraploid species via an artificial tetraploid.

cedures Blank developed cottons that successfully withstood the disease in the field under epidemic conditions, when susceptible varieties were severely damaged.

The initial resistant strains were not entirely acceptable agronomically, but continued backcrossing combined with selection for resistance made it possible, in 1974, to release three primary breeding stocks ('AZ 41', 'AZ 42', and 'AZ 43') with acceptable agronomic properties. Such resistance to cotton rust was previously unknown in *G. hirsutum* L.

Another important disease in most cotton-growing areas of the world is caused by *Xanthomonas malvacearum* (E. F. Smith) Dowson and is variously known as bacterial blight, angular leafspot, and blackarm disease. The development of resistant varieties has concerned workers for many years, a story recently reviewed by Brinkerhoff (*2*). Notable in this history was the pioneering work of R. L. Knight. Beginning in the 1930's he surveyed a broad range of *Gossypium* germplasm, from wild species to cultivated varieties.

Knight isolated a number of sources of resistance and carried out studies to indicate allelism and to determine inheritance patterns. He found both major and minor (or background) genes. Sixteen major genes for blight resistance (table 1) have subsequently been isolated and identified, of which ten derive from *G. hirsutum* L., one from a form of *G. barbadense* L. (probably having some introgression of *G. hirsutum* L. germplasm), and the remainder from the diploid species *G. arboreum* L., *G. herbaceum* L., and *G. anomalum* Wawr. & Peyr. Other of the wild diploid species have been shown to be resistant, but specific genes have not been isolated.

TABLE 1.—B *genes carrying resistance to bacterial blight*

Gene symbol	Source of resistance
B_1	*G. hirsutum*
B_2	*G. hirsutum*
B_3	*G. hirsutum* var. *punctatum*
B_4	*G. arboreum*
B_5	*G. barbadense*
B_6	*G. arboreum*
B_7	*G. hirsutum*
B_8	*G. anomalum*
B_{9K}	*G. herbaceum*
B_{10K}	*G. hirsutum* var. *punctatum*
B_{9L}	*G. hirsutum*
B_{10L}	*G. hirsutum*
B_{11}	*G. herbaceum*
B_{In}	*G. hirsutum*
B_N	*G. hirsutum*
B_S	*G. hirsutum*

Source: Brinkerhoff (*2*).

The blight disease organism itself is variable and exists as a multiplicity of races differing in virulence. We are thus dealing with a situation of host-pathogen interaction. Indeed, this very interaction, or disease differential, serves as a means of identifying the known genes for resistance. It also complicates the disease problem in the field, as pathologists are well aware, because the bacterium can mutate readily and can rapidly evolve more virulent races, a difficulty generally met by combining genes for resistance at several loci into a single line. This approach, combined with suitable field sanitation, provides good disease control.

From a plant breeder's viewpoint, the problem was first confronted in the Sudan, where the varieties of *G. barbadense* L. in production had no resistance to the disease. Blight-resistance genes had to be introduced from outside the species, and as many as 16 backcrosses were required to recover the desired fiber properties of the recurrent parent. Nevertheless, this long-term project was successful, and now a large number of advanced breeding strains, all carrying one or more genes for resistance (usually B_2 and B_3) are available. Thus, the synthesis of new resistant cultivars in the future will be facilitated. Since about 1965, resistant cultivars have essentially replaced susceptible ones in this area.

In other parts of Africa and in the United States, efforts have been devoted to developing blight-resistant types of *G. hirsutum* L. Some of the early releases were unsatisfactory because their resistance was based on gene B_7, which conferred relatively little resistance and quickly became susceptible under field conditions when the pathogen evolved more virulent races. Newer releases have involved other genes for resistance, including B_2 and B_3 reintroduced from the resistant Sudan varieties of *G. barbadense* L. Screening techniques involving mixtures of the more virulent strains of the pathogen have also raised the effectiveness of the polygenic background to these major genes. A number of blight-resistant varieties of *G. hir-*

sutum L. are now in commercial production.

But the germpool has been used for other purposes than as a source of resistance. Certain specific morphological characters, often simply inherited, are agriculturally desirable. Kohel has published a detailed review of the agronomic properties of five such genetic variants (*6*).

One example concerns plant pubescence. The development of very dense pubescence was found to be an effective method of controlling jassids in cotton-growing areas of Africa. Knight and other workers developed hairy varieties of *G. hirsutum* L. that effectively resist these insects. A single major gene, H_1, is responsible for the desired phenotype. Where jassids are important pests of cotton, such highly pubescent varieties are now commonly grown. The same pubescent phenotype may also provide resistance to the fleahopper.

In other cotton-growing areas, however, jassids are not pests, and dense pubescence may not be desirable. Some insects, in fact, require plant hairs for egg laying, and their numbers are significantly reduced on completely glabrous strains of cotton.

The presence or absence of plant hairs is also important in large-scale mechanical harvesting. The hairs on most cotton varieties cause bracts, leaves, and leaf fragments to become entangled with the cotton fibers at harvest. This "leaf trash" lowers the grade of harvested cotton and is difficult and costly to remove in subsequent processing.

For these reasons there has been considerable interest in the genetics of plant pubescence and in the development of cottons of varying degrees of hairiness, from the completely glabrous or nearly glabrous smooth-leaf cottons to the hirsute, jassid-resistant types. Lee found, in *G. hirsutum* L., at least three independent loci concerned with the phenotypic development or suppression of plant hairs (*7*). Certain of these alleles have been introduced into Upland cottons from primitive races of *G. hirsutum* L.—in the case of D$_2$–Smoothleaf, from the diploid *G. armourianum* Kearn. (*10*)—giving rise in some instances to agricultural varieties and in others to primary breeding stocks.

POLYGENIC CHARACTERS

The breeding of polygenic, complexly inherited traits into cultivated cottons is a more difficult problem. A good example is the effort to develop cottons with high fiber-strength from a variety of sources, principally the primitive Hopi cultivar and the so-called Triple Hybrid material. The Triple Hybrid resulted from crosses made by J. O. Beasley in the 1930's between the diploid species *G. thurberi* Tod. and *G. arboreum* L., which after doubling to the tetraploid level was then crossed to the tetraploid *G. hirsutum* L. (fig. 3). The resulting hybrid thus involved three species, was tetraploid, and had sufficient fertility to permit subsequent backcrossing to *G. hirsutum* L. Although the Triple Hybrid material was a source of high fiber-strength, presumed to derive from the *G. thurberi* Tod. germplasm, the high fiber-strength was, however, closely correlated with low lint production. The problem of introducing this desirable germplasm into agronomically desirable cottons was therefore not entirely successful at first.

The most intensive and successful attempt to do this was the program carried out in South Carolina and reported by Culp and Harrell (*3, 4*). These authors give detailed pedigrees that illustrate the complexity of the history of the high-strength cottons they have developed. During 38 years of intercrossing, outcrossing, and selection, significant advances were made in raising the productivity of the experimental material to the level of the check variety while retaining a higher level of fiber and yarn strength. This work culminated in the release

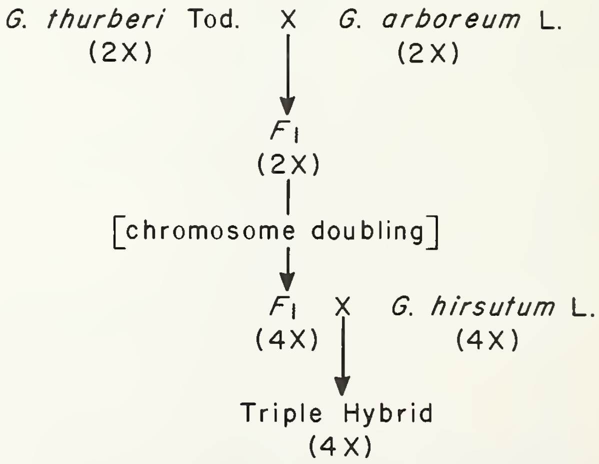

FIGURE 3.—Pedigree of Triple Hybrid material.

of several breeding lines that have fiber and yarn strength in the range of 110 to 120 percent of the current check varieties.

The root-knot nematode *(Meloidogyne incognita acrita)* causes serious cotton crop losses over a wide area. These organisms are parasitic on cotton roots and cause a significant disruption of normal root function. In addition, the damage to the root system provides an entrance for other soil-borne disease organisms, notably *Fusarium*. It is therefore appropriate to speak of damage resulting from the root-knot nematode-*Fusarium* disease complex.

This disease complex in the U.S. Cotton Belt was recognized and described as early as 1892, and since that time cotton breeders have attempted to develop resistant varieties. In 1952, with the release of 'Auburn 56', they achieved the most resistant commercial variety then available, although it was only moderately resistant.

Subsequently, work was undertaken by A. L. Smith, J. E. Jones, and R. L. Shepherd with a primitive race stock, of uncertain origin but reputed to have come from Mexico, that was found to be moderately resistant to the root-knot nematode. A pedigree breeding program, coupled with efficient greenhouse screening for nematode resistance, in which materials were advanced from the F_6 through the F_{10} generations, resulted in the isolation of two highly resistant F_{10} lines. In fact, their resistance is greater than anything previously known, and they are regarded as transgressive segregants (*15*). One of these has been released as a primary breeding stock named 'Auburn 623 RNR' (*16*). It has been found that controlling nematode infestation by using these resistant varieties also results in satisfactory control of *Fusarium* wilt.

No story of germpool manipulation in *Gossypium* would be complete without a reference to glandless cottons. Gossypol glands are distinctive structures found in all species of *Gossypium* and in certain related genera. They are scattered throughout most of the above-ground parts of the plant and contain gossypol and related triterpenoid compounds and often other pigments as well. The gossypol in the glands of the embryo of the seed is an undesirable or toxic constituent of the oil pressed from the seeds and of the protein-rich meal remaining after oil extraction. The glandless genotypes discovered by McMichael in the 1950's (*8*, *9*), were therefore recognized as having agricultural importance, because glandless plants produce seeds having no gossypol glands and very little gossypol in the embryos.

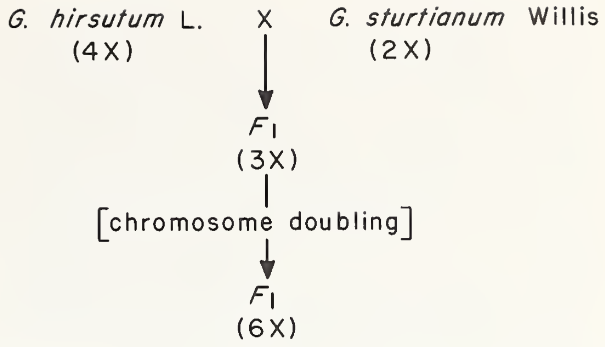

FIGURE 4.—Pedigree of Muramoto's hexaploid cottons.

Subsequent work by geneticists and plant breeders resulted in the development of commercially successful glandless cottons. It should be emphasized that these glandless genotypes were achieved by the genetic manipulation of materials from a variety of sources within the *Gossypium hirsutum* L. germpool, including the Hopi cotton cultivated in pre-Columbian times by the Pueblo Indians. The result is a plant having a phenotype (glandless) previously unknown in the entire genus *Gossypium*, and a plant that is not only a source of fiber but a source of oil essentially free of discoloring pigments and an important potential new source of protein for human consumption.

A problem with glandless cottons was soon discovered. Certain insects not normally pests of cotton attacked glandless cotton; other insects, such as *Lygus* bugs, were more damaging to glandless than to normal cotton. Apparently gossypol inhibited the feeding of these insects on normal cotton. But in the problem was potential: a source of built-in resistance to phytophagous insects. Again drawing on the *Gossypium* germpool, breeders have found sources of increased gossypol and have developed new types of cotton having high levels of gossypol in their tissues.

So the development of glandless cottons has resulted in the breeding of both high-gossypol and low-gossypol (glandless) cottons, the one having advantages in production, the other in processing. What remains for breeders to do, in my opinion, is to combine these two advantages in the same cotton plant, a plant having glands and high levels of gossypol in all parts except the embryo. Such a combination is biologically possible, because it is already known to exist in several wild species (e.g., *Gossypium bickii* Prokh.) and in the related genus *Cienfuegosia*. It is thus less of a genetic challenge than was the isolation of the completely glandless phenotype in the first place. It would have even greater agricultural significance.

EXOTIC USES OF THE GERMPOOL

The *Gossypium* germpool has also been put to certain exotic uses that may be regarded both as concrete accomplishments already achieved and as achievements with potential for the future. Two examples will be given.

In a unique series of experiments, Muramoto (*14*) produced new hexaploid breeding stocks by crossing tetraploid *G. hirsutum* L. with the wild diploid *G. sturtianum* J. H. Willis and then doubling the chromosome number of the resulting triploid hybrid (fig. 4). The hexaploid plants so obtained had rather limited fertility at first, but continued selection over many generations significantly raised the level of fertility. At the same time, fiber length and fiber quantity have been improved by selection. Three noncommercial breeding stocks ('Arizona 6X–3', 'Arizona 6X–13', and 'Arizona 6X–50') were released in 1974. This material at the present time is more of a novelty than an agricultural achievement, but it nevertheless clearly demonstrates that specific characteristics of the wild species (e.g., the cold tolerance of *G. sturtianum* J. H. Willis and resistance to certain insects) can be incorporated into lint-bearing cottons. It also demonstrates the feasibility of exploring new ploidy levels in long-term plant-breeding experiments and of utilizing the entire genomes of the diploid species at these new ploidy levels. Similar experiments using other wild diploids have yet to be initiated.

Another line of exotic experimentation with the germpool concerns the manipulation of various cytoplasms, quite apart from the genetic content of the nuclei. This line of work had its initial impetus in the search for cytoplasmic control of male sterility (*11*). More recently it has taken on importance in relation to potential disease resistance, following the corn blight epidemic on *Zea* and the realization that cytoplasmic factors may be of great importance in such areas as disease resistance.

In *Gossypium*, work on cytoplastic manipulation has been carried on most vigorously by V. G. Meyer. Her work resulted in the release of 16 experimental breeding lines (*12*) that combine the nuclear gene complement of two different Upland cottons ('Delcot 277' and 'Deltapine 16', both *G. hirsutum* L.) in various combinations with cytoplasms of seven other species of *Gossypium*. These experimental lines were developed with modified backcrossing in which the sources of cytoplasm were the tetraploid species *G. barbadense* L. and *G. tomentosum* Nutt. ex Seem. and the diploid species *G. herbaceum* L., *G. arboreum* L., *G. anomalum* Wawr. & Peyr., *G. harknessii* Brandg., and *G. longicalyx* Hutch. & Lee. These experimental lines provide a valuable and unusual new source of germplasm, of potential value in solving applied agricultural problems. These materials are currently undergoing screening tests for such things as cold tolerance, disease and insect resistance, and response to pesticides. Their specific value or utility remains conjectural, but their development greatly broadens the germplasm base of *Gossypium*. Data already available shows the significant genetic effects of these various cytoplasms.

In conclusion I wish to point out that the germpool in *Gossypium*, which is very broad, has been successfully used to accomplish a variety of objectives, and it remains of immense potential value for the future. The germpool has been a source of desirable genes that have been transferred from primitive types or wild species into agriculturally valuable cottons. Of especial interest and importance have been those cases where the germpool has been used creatively to produce plants that were previously unknown. Examples include Upland cottons resistant to cotton rust, the transgressive segregants for nematode resistance, and the whole range of glandless cottons, a phenotype previously unknown in the genus. Such examples provide the impetus for believing that many more creative possibilities exist in utilizing the germpool of *Gossypium* and emphasize the value of maintaining and expanding it.

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